

Transport and growth of larval cisco (*Coregonus artedii*) in the Keweenaw Current region of Lake Superior

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Abstract: Larval cisco (*Coregonus artedii*) were sampled from Lake Superior off the western coast of the Keweenaw Peninsula (Michigan, USA) to determine if the Keweenaw Current influences their distribution and growth. Bongo net tows were conducted during April–June 2000 from four transects extending from 0.1 to 17 km offshore. For most sampling dates, cisco tended to be slightly more abundant, larger, and older at inshore locations. Later-hatched larvae appeared at the western-most transects first, during which time earlier-hatched larvae disappeared from the study area. This pattern followed what would be expected if larvae were being transported eastward by the prevailing Keweenaw Current. Estimated growth rates were 84% higher for later-hatched compared with earlier-hatched larvae and 25% lower for offshore larvae from the eastern-most transects compared with elsewhere. Accordingly, surface water temperatures partly explained spatial and temporal variations in growth rate. These results indicate that cisco larvae in Lake Superior may be transported great distances from major spawning sites by longshore currents and that the temperature regime of nursery areas may largely control their growth.

Résumé : Nous avons échantillonné des larves de ciscos de lac (*Coregonus artedii*) du lac Supérieur au large de la côte occidentale de la péninsule de Keweenaw (Michigan, É.-U.) afin de déterminer si le courant de Keweenaw affecte leur répartition et leur croissance. Nous avons effectué des traits de filets bongo en avril–juin 2000 sur quatre transects allant de 0,1 à 17 km de la rive. Pour la plupart des dates d'échantillonnage, les ciscos avaient tendance à être légèrement plus abondants, plus grands et plus vieux dans les sites près de la rive. Les larves à éclosion plus tardive apparaissent d'abord dans le transect situé le plus à l'ouest, au moment où les larves à éclosion plus hâtive ont disparu de la zone d'étude. Ce patron s'accorde avec ce qu'on peut attendre si les larves sont transportées vers l'est par le courant prédominant de Keweenaw. Les taux de croissance estimés chez les larves à éclosion tardive sont 84 % plus élevés que ceux des larves à éclosion hâtive et ils sont de 25 % inférieurs chez les larves du large dans le transect le plus à l'est par comparaison à tous les autres sites. En conséquence, les températures des eaux superficielles expliquent en partie les variations spatiales et temporelles des taux de croissance. Nos résultats indiquent que les larves de ciscos du lac Supérieur peuvent être transportées sur de longues distances à partir des principaux sites de fraye par les courants côtiers et que les régimes thermiques des zones de nourricerie peuvent en grande mesure contrôler leur croissance.

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Introduction

Cisco (*Coregonus artedii*) in Lake Superior declined precipitously in the 1960s, resulting largely from sequential overfishing of discrete stocks (Lawrie and Rahrer 1973; Selgeby 1982). Decades of harvest regulation have allowed cisco stocks to rebound, but recovery has been slow and largely inhibited by highly variable recruitment (Bronte et al. 2003; Hoff 2004).

Cisco recruitment appears to be controlled by a combination of biotic and abiotic factors. Within US waters of Lake

Superior, Kinnunen (1997) found that the spatial abundance of yearlings was positively correlated with surface water temperatures during their first 2 months of life. However, annual fluctuations were greater than spatial variations (Kinnunen 1997). Accordingly, recruitment success tends to be synchronized among the different stocks across the lake, independent of stock size (Bronte et al. 2003). In Wisconsin waters of Lake Superior, Hoff (2004) concluded that recruitment was suppressed by slimy sculpin (*Cottus cognatus*) predation on eggs, lake trout (*Salvelinus namaycush*) predation on young of the year, and adult cisco predation on their young, which interestingly was alleviated by higher wind speeds during the month of hatching.

Hoff's (2004) results imply that wind-driven currents may be important for reducing predation by dispersing larvae away from major spawning sites. Dispersal, especially by currents, would force larvae to encounter varying environmental conditions that could either favorably or adversely influence growth and survival.

Marine studies have long addressed the importance of hydrodynamic processes on recruitment (Norcross and Shaw 1984). Many marine fishes have been found to rely on cur-

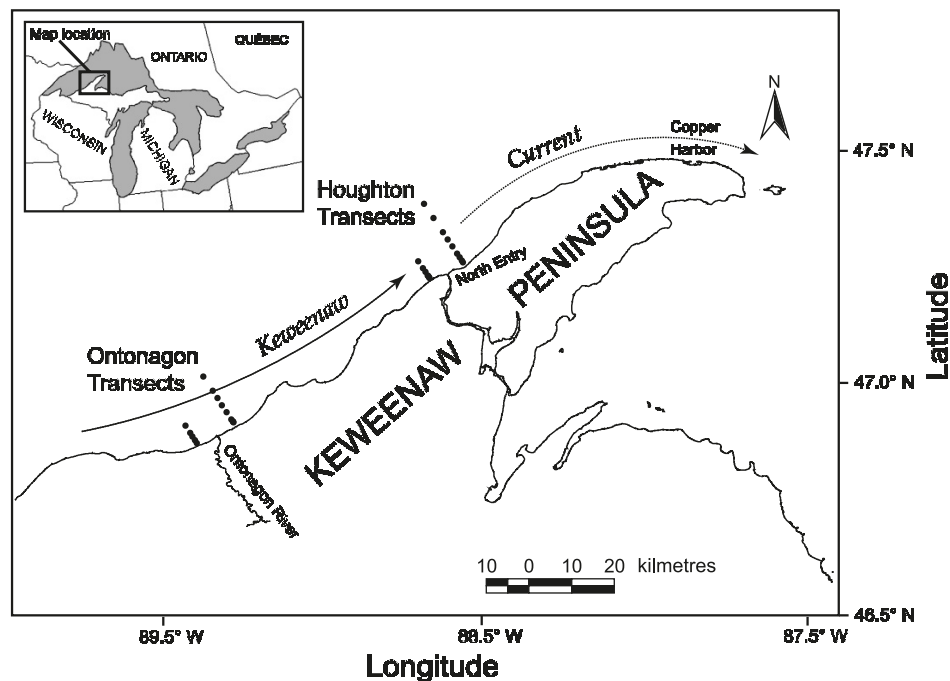
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Fig. 1. Study area in Lake Superior showing the four sampling transects off the western coast of the Keweenaw Peninsula, Michigan, USA.



rents, upwellings, or riverine discharges to transport eggs or larvae from spawning grounds to nursery habitats (Norcross and Shaw 1984; Werner 2002). Consequently, anomalies in the regularity of large-scale hydrodynamic patterns may cause periodic recruitment failures (Cowan and Shaw 2002).

Freshwater lakes usually lack strong and predictable currents (Werner 2002; Moyle and Cech 2004), but the Great Lakes are large enough to exhibit oceanographic processes (Ullman et al. 1998; Beletsky et al. 1999). In particular, very large lakes tend to have regular currents in the form of a gyre (Hutchinson 1957). In Lake Superior, circulation is generally counterclockwise, with the Keweenaw Current being a particularly strong current traveling northeasterly along the western coast of the Keweenaw Peninsula, Michigan (Lam 1978; Beletsky et al. 1999). Velocities of this current can exceed $75 \text{ cm}\cdot\text{s}^{-1}$ in July (Niebauer et al. 1977). Despite the presence of strong and regular currents in Lake Superior, the importance of current-driven transport on cisco recruitment is unknown. The objective of this study was to determine how transport within the Keweenaw Current region of Lake Superior affects larval cisco distribution and growth, as it may relate to recruitment dynamics.

Materials and methods

Field sampling

Larval cisco were sampled from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan, USA, during six cruises from April to June 2000. Net tows were conducted from four transects (Ontonagon North and South, and Houghton North and South) that ran perpendicular to the coast (Fig. 1). Dual, 70 cm diameter, 500 μm mesh bongo nets were employed to collect two samples per tow. A flow meter recorded the volume of water filtered per net. From the transects, four–nine tows were conducted from 0.1 to 17 km from shore. Locations and numbers of tows

conducted varied among transects and cruises because of weather and time constraints. At each distance from shore, one tow filtered surface (top 1 m) water at a speed of $0.77\text{--}1.03 \text{ m}\cdot\text{s}^{-1}$ (1.5–2.0 knots) for 15 min, thus filtering on average (\pm standard deviation, SD) $217.3 (\pm 76.3) \text{ m}^3$ of water per net. The nets were towed parallel with shore (except for the first cruise when they were towed perpendicularly) during daylight (except for 21 May at Houghton North).

A total of 158 samples were collected with 79 tows: 28 tows from the Ontonagon transects and 51 tows from the Houghton transects. Samples were preserved with 95% ethanol so otoliths would be preserved for age analysis. A Sea-Bird Electronics conductivity–temperature–depth (CTD) meter (SBE-25) or a Hydrolab MiniSoude was used to measure vertical temperature profiles at the start of each tow and sometimes from additional distances from shore.

Laboratory measurements and otolith analysis

To determine spatial patterns in growth and development, several morphological characteristics of larval cisco were measured. In the laboratory, cisco were first separated from the samples and stored in 70% ethanol. Total length of all larvae was measured to the nearest 0.05 mm with a dial caliper. For a subsample of five randomly selected larvae per sample, or the entire sample when five or less larvae were captured, caudal fin rays were counted, and yolk depth and length were measured to the nearest 0.01 mm at $0.9\times\text{--}2.0\times$ magnification using a dissecting microscope equipped with an ocular micrometer. As an indicator of energy reserves, yolk measurements were used to calculate yolk sac volume, assuming a prolate spheroid with length as the longer axis and depth and girth as the shorter and equal axes (Luczynski et al. 1986). The number of caudal fin rays was used as an indicator of developmental stage, knowing that larvae hatch with no fin rays and progressively develop up to 28 caudal fin rays when juveniles (Hinrichs and Brooke 1975). Total

length (TL) and yolk volume (YV) were corrected for preservation-induced shrinkage (for preservation in 70% ethanol) with linear regressions developed from laboratory-reared cisco: live TL = $1.20 + 0.91 \times \text{preserved TL}$ and live YV = $0.50 + 0.96 \times \text{preserved YV}$ (Oyadomari 2005).

Ages, in days, of the five randomly selected cisco per sample were estimated from otoliths following the procedures of a joint otolith validation study (Oyadomari and Auer 2007). Left and right sagittae were removed with needles under a dissecting microscope equipped with a polarizing filter. Dissected otoliths were then transferred to a microscope slide and mounted concave side down with CrystalBond (SPI Supplies), a thermoplastic mounting medium. The number of otolith increments after check formation was counted under a compound microscope using up to 1000 \times magnification, and counts from left and right sagittae were averaged for each larva. Age in days was then calculated from the number of otolith increments (i.e., rings) with a linear regression developed from laboratory-reared cisco: age = $28.09 + 1.04 \times \text{rings}$ (Oyadomari and Auer 2007). Age was further used to calculate hatch dates by subtracting age from date of capture.

In order to estimate the growth rate for the last 5 days before capture using the biological intercept procedure (Campana 1990; Campana and Jones 1992), a linear relationship between fish length and otolith size had to be established, and fish length and otolith size at the biological intercept had to be determined. Otolith radius was measured as a metric of otolith size. Because cisco otoliths form from multiple primordia (Oyadomari and Auer 2007), and because having multiple primordia increases the variability in otolith nuclear dimensions (Neilson et al. 1985), the radius was measured from the posterior edge to the check mark; thus, the nuclear region was excluded. Otoliths were measured from digitally captured images with a computer image-analysis program (SigmaScan Pro 5; SPSS Inc., Chicago, Illinois), and measurements from left and right sagittae were averaged. The TL to otolith radius (RA) relationship was curvilinear, so otolith radius was square-root transformed ($\sqrt{\text{RA}}$) to produce a linear relationship: TL = $8.8 + 1.31 \times \sqrt{\text{RA}}$ ($n = 111$, $r^2 = 0.80$, $P < 0.0001$). In this case, the biological intercept represented the point of check formation, during which the otolith radius would be zero. When there was a 50% likelihood that a larva contained a check mark, larval TL was estimated to be 11.04 mm (with 95% Fieller bounds of [10.64, 11.32]) with probit analysis ($n = 232$, $P < 0.0001$) (Tabachnick and Fidell 1996). Fish length at previous age a could now be estimated with the following equation: $L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$, where L_a is fish length at previous age a , O_a is otolith size at previous age a , L_c is fish length at capture, O_c is otolith size at capture, L_o is fish length at the biological intercept, and O_o is otolith size at the biological intercept (Campana 1990). Using this equation, larval length at 5 days before capture was predicted with square-root transformed radial length that excluded the last five increments. Finally, increase in TL during the last 5 days was expressed as a daily growth rate. For comparison, the average lifetime growth rate was also calculated for groups of larvae with length-to-age linear regressions, wherein the slope represented the daily growth rate. These two measures of growth not only differ in temporal coverage

(lifetime vs. last 5 days), but also in the pool of larvae that could be employed. For recent growth, larvae had to have at least five increments, while for length-to-age growth, larvae only had to have a check mark.

Data analysis

Of the six sampling cruises during 2000, four (15–17 May, 21 May, 30 May, and 19–20 June) captured sufficient numbers of larval cisco for statistical analyses. Preliminary analyses did not show statistical differences between the north and south transects of either Ontonagon or Houghton. Accordingly, data from the two transects were pooled into a region for Ontonagon and a region for Houghton for all subsequent analyses. For some analyses, it was necessary to pool adjacent distances from shore into three transect divisions (0.1–2, 3–5, and 7–17 km from shore) to increase sample sizes. These divisions spanned different ranges so that there would be greater spatial resolution nearer to shore.

Offshore trends in density were modeled separately for each region and cruise with a posteriori curve fitting. Spatial differences in larval fish characteristics were assessed separately for each cruise with multiple linear regressions for cruises with both regions sampled and simple linear regressions for cruises with only one region sampled.

For 26% of the larvae for which otoliths were examined, age could not be estimated with otolith analysis because they had yet to produce a check mark. For these larvae, age was estimated with age-to-length linear regressions generated with data from the same cruise, region, and transect division. Although these estimated ages were probably not as accurate as ages estimated directly by otolith analysis, it was important to incorporate the younger larvae into calculations of mean age so that these means would not be biased toward the older larvae.

Hatch dates were not compared among distances from shore for each region and cruise, as described previously for the other metrics, because hatch dates are linearly dependent upon capture date (cruise) and age. Such an analysis would only show transposed results from that of age. Instead, hatch dates were compared among cruises, separately by region, with single-factor analysis of variance (ANOVA), wherein all distances from shore were pooled. However, because not all larvae of large samples were aged with otolith analysis, larger samples would be under-represented in pooled means if subsample means were weighted by their subsample sizes. Accordingly, subsample sizes were adjusted so that they were the same proportions of their total subsample size as capture numbers (from which subsamples were drawn) were to their total sample size while still maintaining the same total subsample size. In this manner, pooled means should reflect pooled populations and will not be biased by subsample sizes being unequally proportional to capture numbers. Hatch dates were also grouped into three hatch periods (early-hatch: 22 March – 8 April; bulk-hatch: 9 April – 26 April; and late-hatch: 27 April – 17 May) for some analyses. These categories included an estimated 9%, 81%, and 10%, respectively, of all captured larvae.

For each cruise, the movement or transport of larvae was assessed by graphically displaying the percentages of larvae from each hatch period for each region, transect division,

and sampling cruise. This allowed for the assessment of where recently hatched larvae first appeared and where earlier-hatched larvae last appeared, as well as the spatial and temporal progression of recently hatched larvae replacing earlier-hatched larvae.

Growth rates estimated by length-to-age relationships were analyzed for spatial and hatch date differences with multiple regressions (Neter et al. 1996). Spatial differences were assessed by determining if the length-to-age slope varied with region and distance from shore, while hatch date differences were assessed by determining if slope varied with hatch period. Spatial differences were also assessed for back-calculated recent growth by determining if the growth rate varied with region or distance from shore (Neter et al. 1996). Age needed to be included as an independent variable in this model as well, because growth rates are typically dependent on age, and mean ages can vary spatially. Larvae for which age was estimated with total length because they were too young to age with otolith analysis were excluded from the growth rate analyses.

To determine if spatial differences in growth rates were correlated with spatial differences in temperature, growth rates were regressed on water temperature for each region. Furthermore, a temperature threshold, below which temperature was proposed to inhibit growth, was estimated by dividing the data set repeatedly by different temperatures, in 0.5 °C increments from 7 to 9 °C, instead of by region, then observing at what temperature the greatest inhibitory effect existed below it. Statistical analyses were performed with SYSTAT 10 (SPSS Inc., Chicago, Illinois), except for nonlinear regressions, which were performed with SigmaPlot 8 (SPSS Inc.).

Results

Seasonal occurrence of cisco

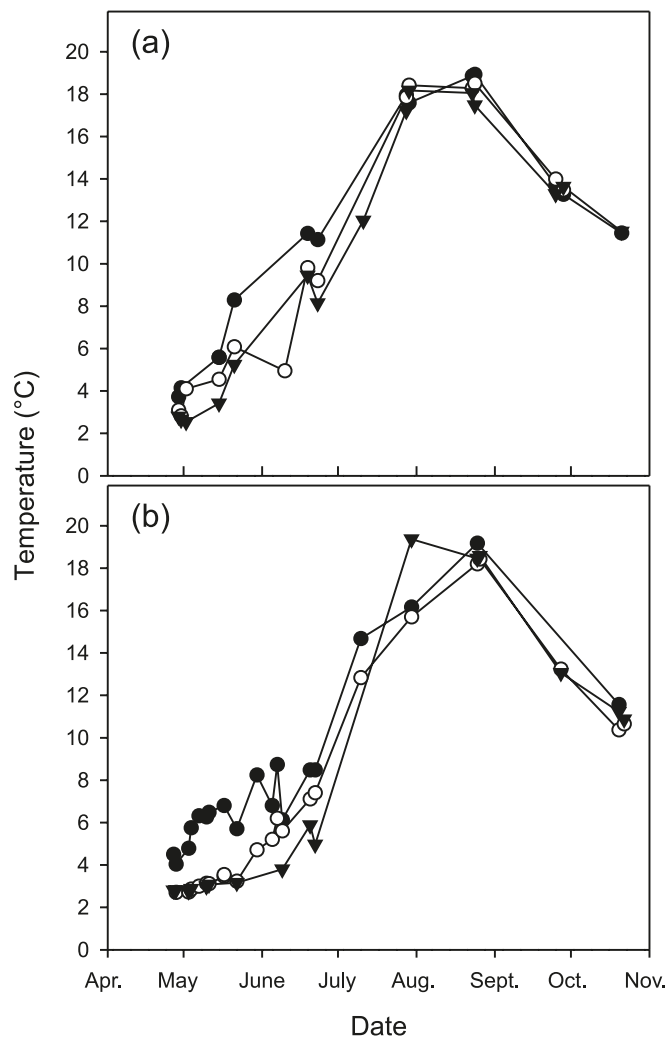
The sampling season commenced before the bulk of the hatch and extended to the time when larvae became rare. During the first cruise (27–29 April), surface water temperatures averaged 3.1 °C (range: 2.5–4.5 °C) (Fig. 2), and only two larval cisco were captured with 20 samples (overall mean density of 2.5 larvae·(1000 m³)⁻¹). The highest densities (overall mean density of 77.0 larvae·(1000 m³)⁻¹) of cisco were obtained during the second half of May, when temperatures averaged 6.0 °C (range: 3.1–8.5 °C). Catches greatly diminished by June (overall mean density of 3.4 larvae·(1000 m³)⁻¹), when temperatures averaged 8.2 °C (range 4.6–11.4 °C), although there were great spatial differences in abundance during this period.

Spatial distribution in temperature, density, and larval fish size

As expected, surface water temperatures decreased with distance from shore for all cruises, and the shallower waters at Ontonagon fostered higher temperatures than those at Houghton from 21 May onward (Fig. 3). Surface waters of less than 4 °C were still observed at Houghton on 21 May from 5 km outward and on 30 May from 7 km outward, but not at Ontonagon up to 13 km from shore on 21 May.

By the second cruise, 15–17 May, cisco catches were sufficient for statistical analyses. Cisco densities during this

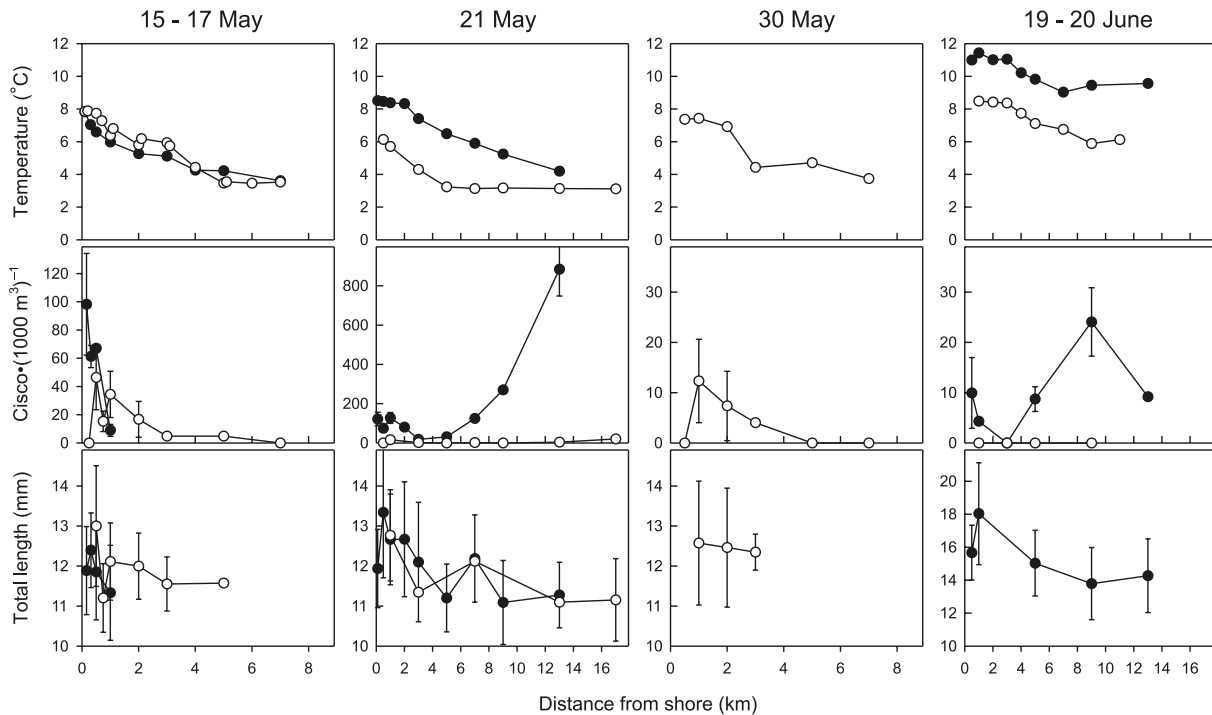
Fig. 2. Seasonal changes in surface water temperature in 2000 at 1 km (●), 5 km (○), and 9 km (▼) offshore on the (a) Ontonagon North and (b) Houghton North transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.



cruise decreased linearly with distance from shore at Ontonagon (linear regression: $n = 8$, $r^2 = 0.79$, $P = 0.003$), but at Houghton, offshore densities most closely followed a log-normal trend (lognormal regression: $n = 28$, $r^2 = 0.45$, $P = 0.001$) because of zero catches at 0.25 km from shore (Fig. 3). Total lengths of larvae (multiple regression: $n = 187$, $r^2 = 0.07$), however, did not differ with region ($P = 0.06$), distance from shore ($P = 0.20$), or the interaction ($P = 0.90$) (Fig. 3).

During the next cruise, 21 May, we sampled to a much farther offshore extent at both Ontonagon and Houghton than previously. At Ontonagon, there were greater densities inshore than offshore up to 5 km from shore, but beyond that, we encountered a high-density patch of cisco extending to at least 13 km from shore (Fig. 3). Therefore, the offshore trend in density closely followed a quadratic equation (quadratic regression: $n = 24$, $r^2 = 0.97$, $P < 0.0001$). At Houghton, the trend was similarly quadratic (quadratic regression: $n = 16$, $r^2 = 0.52$, $P = 0.009$), although densities were substantially lower, which may have resulted, in part, from these samples being collected at night. In contrast

Fig. 3. Offshore trends in surface water temperature and mean (\pm standard deviation, SD) density and total length (TL) of larval cisco (*Coregonus artedii*) collected during four sampling cruises in 2000 from the Ontonagon (●) and Houghton (○) transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.



with the previous cruise, total lengths of larvae (multiple regression: $n = 1035$, $r^2 = 0.21$) now decreased with distance from shore ($P < 0.0001$), but did not differ between regions ($P = 0.66$) or for the interaction ($P = 0.81$) (Fig. 3).

On 30 May, only Houghton was sampled, and sampling extended to the same offshore extent (7 km) as for the 15–17 May cruise. By this time, densities had greatly diminished, yet interestingly, they exhibited a similar lognormal trend as previously (lognormal regression: $n = 18$, $r^2 = 0.54$, $P = 0.003$), with no larvae captured at 0.5 km from shore. Total length also did not differ with offshore distance (linear regression: $n = 21$, $r^2 = 0.003$, $P = 0.81$) (Fig. 3).

On 5–7 June, sampling was conducted only at Houghton, and only seven cisco were captured in 26 samples, so these data are not presented. On the last cruise, 19–20 June, larvae were captured only at Ontonagon. The distribution of these larvae was scattered, with peaks at 0.5–1.0 km and at 9 km from shore (Fig. 3). For total length, a decreasing trend with distance from shore was still evident (linear regression: $n = 25$, $r^2 = 0.16$, $P = 0.04$) (Fig. 3).

Spatial distribution in age, yolk volume, and number of caudal fin rays

Estimated ages decreased with distance from shore on 21 May (multiple regression: $n = 116$, $r^2 = 0.24$, $P < 0.0001$ for distance from shore, $P = 0.71$ for region, $P = 0.22$ for the interaction) and 19–20 June (linear regression: $n = 22$, $r^2 = 0.20$, $P = 0.04$) (Fig. 4). For the two cruises during which total length did not differ with distance from shore, age also did not differ with distance from shore (15–17 May, multiple regression: $n = 89$, $r^2 = 0.04$, $P = 0.81$ for distance from

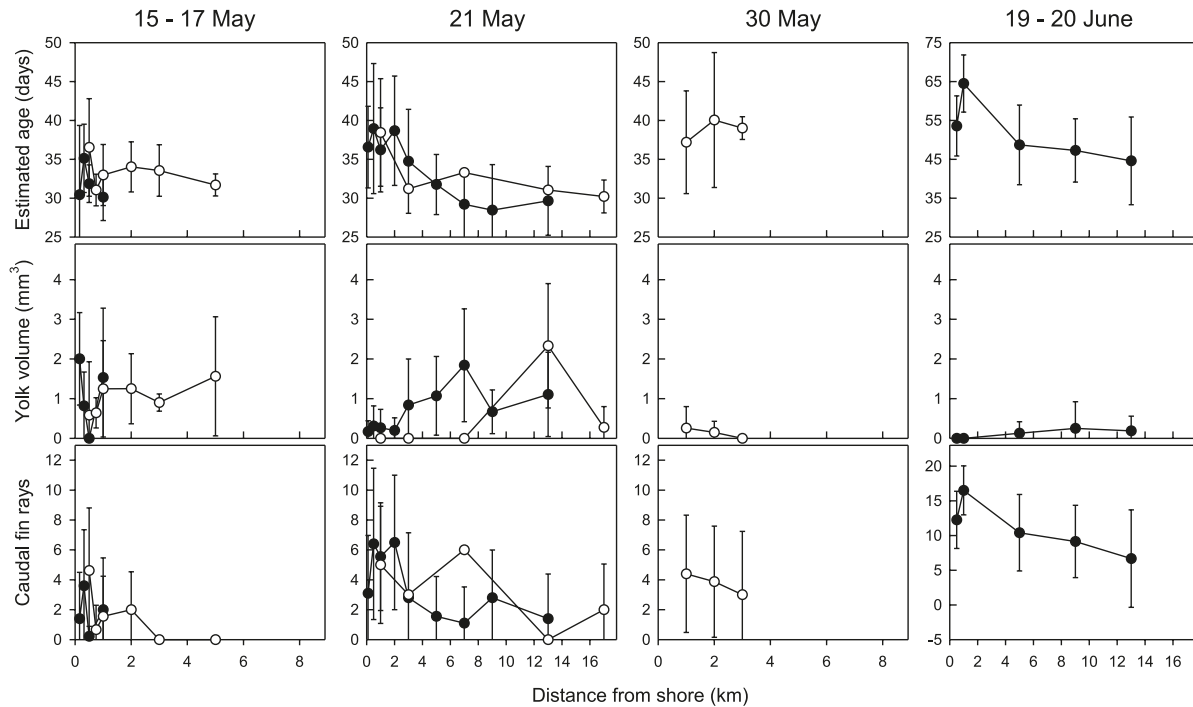
shore, $P = 0.23$ for region, $P = 0.91$ for the interaction; 30 May, linear regression: $n = 20$, $r^2 = 0.02$, $P = 0.51$) (Fig. 4).

The offshore distribution for yolk volume and number of caudal fin rays support the trends observed for age. When age decreased with distance from shore on 21 May, there was a tendency for offshore larvae to have greater yolk volumes (multiple regression: $n = 129$, $r^2 = 0.13$, $P = 0.001$ for distance from shore, $P = 0.41$ for region, $P = 0.16$ for the interaction) and fewer caudal fin rays (multiple regression: $n = 129$, $r^2 = 0.12$, $P = 0.0004$ for distance from shore, $P = 0.96$ for region, $P = 0.32$ for the interaction) (Fig. 4). The same was also true for the other cruise with an offshore age trend, 19–20 June, for number of caudal fin rays (linear regression: $n = 21$, $r^2 = 0.19$, $P = 0.05$), but not for yolk volume (linear regression: $n = 22$, $r^2 = 0.04$, $P = 0.36$), although very few larvae still had yolks at this point in the season. Conversely, cruises that did not show an offshore trend for age also did not show an offshore trend for yolk volume (15–17 May, multiple regression: $n = 99$, $r^2 = 0.04$, $P = 0.23$ for distance from shore, $P = 0.10$ for region, $P = 0.09$ for the interaction; 30 May, linear regression: $n = 20$, $r^2 = 0.04$, $P = 0.41$) or for number of caudal fin rays (15–17 May, multiple regression: $n = 98$, $r^2 = 0.06$, $P = 0.46$ for distance from shore, $P = 0.26$ for region, $P = 0.95$ for the interaction; 30 May, linear regression: $n = 20$, $r^2 = 0.01$, $P = 0.62$) (Fig. 4).

Hatching period of cisco

Captured cisco were estimated to have hatched from 22 March to 17 May, with the bulk of the hatch occurring from mid-April to early May. Mean hatch dates increased with cruise for both Ontonagon (single-factor ANOVA:

Fig. 4. Offshore trends in mean (\pm standard deviation, SD) age, yolk volume, and number of caudal fin rays of larval cisco (*Coregonus artedii*) collected during four sampling cruises in 2000 from the Ontonagon (●) and Houghton (○) transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

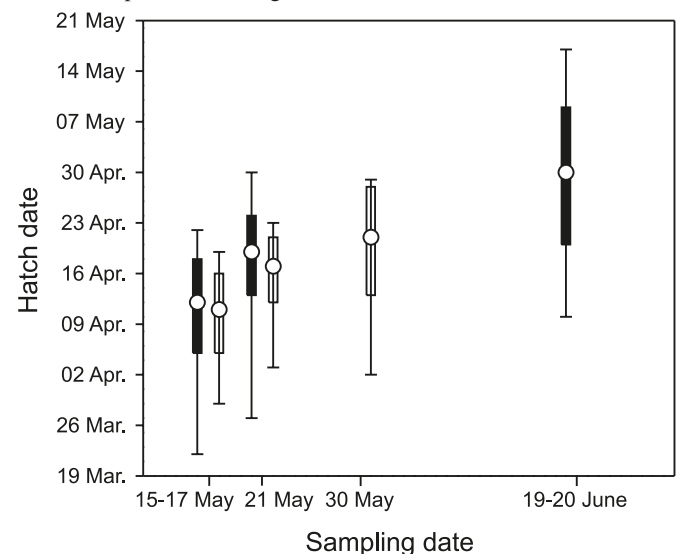


$F_{[2,146]} = 55.68$, $P < 0.0001$) and Houghton (single-factor ANOVA: $F_{[2,95]} = 27.12$, $P < 0.0001$), whereby for both regions, each cruise was statistically different from each other (Tukey's test: least significant comparison, $P < 0.001$ for Ontonagon, $P < 0.05$ for Houghton) (Fig. 5). Correspondingly, the ranges of hatch dates tended to shift toward more recent dates with subsequent cruises (Fig. 5), meaning that early-hatch larvae did not exist in later catches, and late-hatch larvae did not exist in earlier catches, even when most of the late-hatch larvae hatched prior to the earlier sampling dates.

Larval fish transport

Both the higher concentration of younger larvae farther offshore at Ontonagon and the increase in mean hatch date with subsequent sampling cruises could have resulted from larvae being transported through the study region by prevailing currents. Further evidence for larval fish transport was investigated with plots of the percentages of larvae from different hatch periods (early-, bulk-, and late-hatch) for each transect division (0.1–2 km, 3–5 km, and 7–17 km from shore), region (Ontonagon and Houghton), and sampling cruise (Fig. 6). We observed that during 15–17 May, early-hatch larvae composed a small percentage of the inshore catch and late-hatch larvae were not present. During the next cruise, 21 May, early-hatch larvae were still concentrated inshore, and now few late-hatch larvae were encountered offshore, but only at Ontonagon. Late-hatch larvae were encountered at Houghton on 30 May, and by 19–20 June, late-hatch larvae composed approximately half of the catch at Ontonagon, with early-hatch larvae being completely absent in the samples. These patterns show that larvae did not arrive and depart the study region from random

Fig. 5. Hatch date of larval cisco (*Coregonus artedii*) collected during four sampling cruises in 2000 from the Ontonagon (solid bars) and Houghton (open bars) transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Open circles represent the mean, bar limits represent the standard deviation, and whiskers represent the range in hatch dates.



locations, but rather followed the flow of the Keweenaw Current.

Spatial and hatch date differences in growth rates

A length-to-age linear regression for all captured larvae showed an average (\pm standard error, SE) growth rate of $0.18 (\pm 0.008)$ mm·day⁻¹ (Fig. 7). First, this overall growth

Fig. 6. Percentage of larval cisco (*Coregonus artedii*) from each hatch period for each sampling cruise in 2000, transect division, and region in Lake Superior, off the western coast of the Keweenaw Peninsula, Michigan. Hatch periods were 22 March – 8 April for early-hatch (open fill), 9 April – 27 April for bulk-hatch (hatched fill), and 27 April – 17 May for late-hatch (solid fill). Sample sizes are noted above each bar.

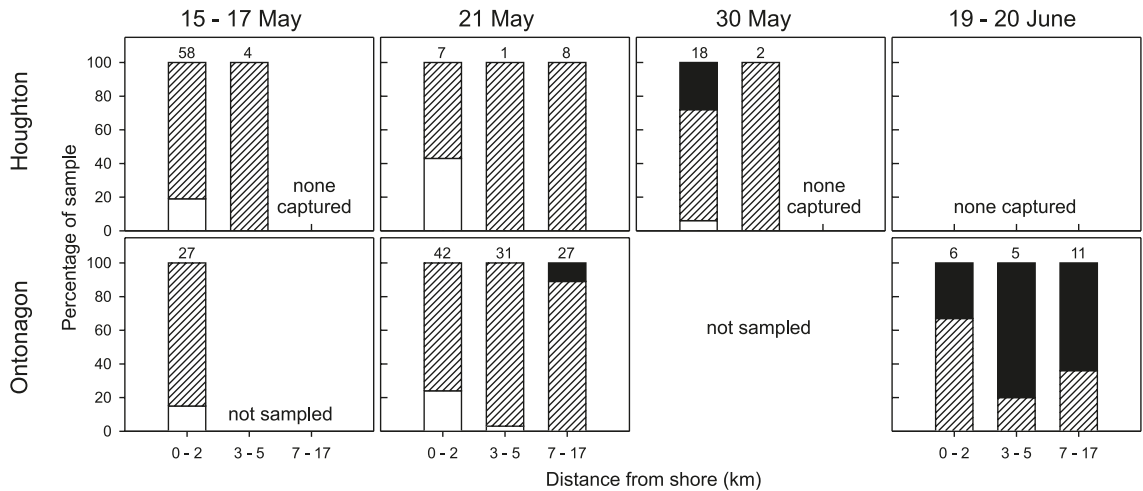
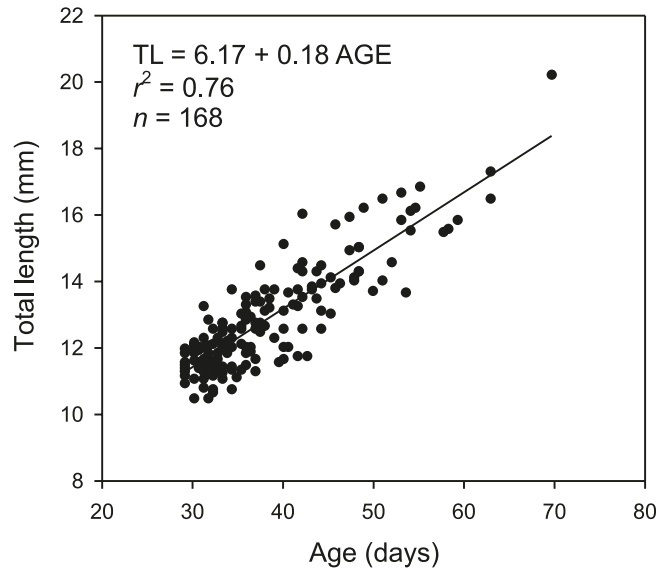


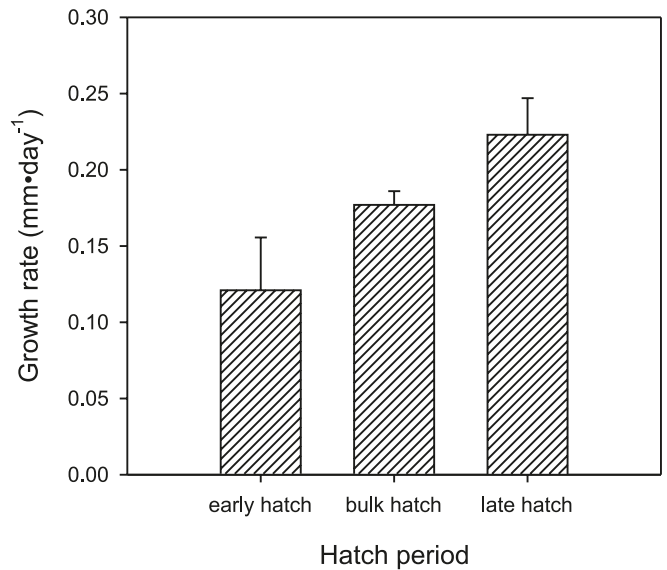
Fig. 7. Total length (TL) to age relationship of larval cisco (*Coregonus artedii*) collected in 2000 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. The slope of the linear regression indicates the overall daily growth rate.



rate was separated by larvae of different hatch periods to determine if late-hatch larvae grew faster because they hatched into, and spend more of their lives in, warmer waters. A multiple regression model for total length as the dependent variable, with age, hatch period, and the interaction as independent variables, showed that the length-to-age relationship was statistically affected by hatch period ($n = 168$, $r^2 = 0.77$, $P = 0.03$ for hatch period \times age interaction). By estimating a separate linear regression for each hatch period, we see that the slope (growth rate) does in fact increase with subsequent hatch periods, as expected (Fig. 8), but only slopes for the early and late hatch periods were statistically different from each other (Tukey's test, $P < 0.01$).

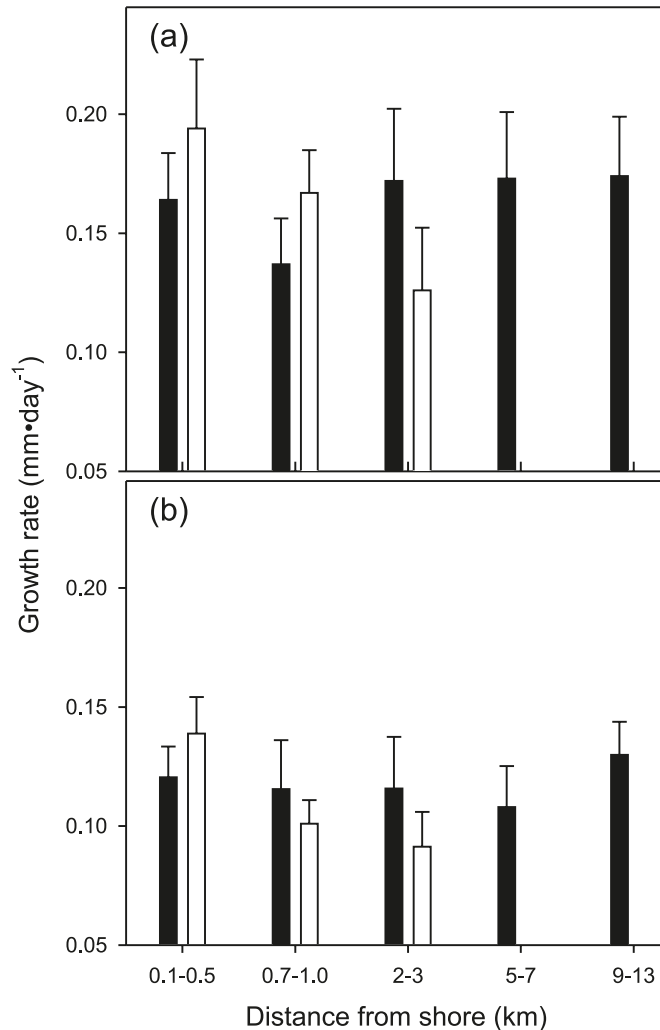
Second, the overall grow rate was separated by larvae of different spatial locations (regions and distances from shore)

Fig. 8. Growth rates (+ standard error, SE) of larval cisco (*Coregonus artedii*) that hatched during the different hatch periods (early-hatch = 22 March – 8 April, bulk-hatch = 9 April – 27 April, and late-hatch = 27 April – 17 May). Growth rates were estimated as the slope of length-to-age linear regressions for larvae collected in 2000 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.



to determine if warmer waters inshore, especially at Ontonagon, fostered faster growth. A multiple regression model ($n = 168$, $r^2 = 0.78$) for total length as the dependent variable, with age, region, distance from shore, and all interactions as independent variables, showed that the length-to-age relationship was statistically affected by distance from shore ($P = 0.02$ for distance from shore \times age interaction) but not by region ($P = 0.19$ for region \times age interaction); however, the effect with distance from shore differed by region ($P = 0.01$ for region \times distance from shore \times age interaction). Growth rates were calculated directly from the data as slopes of separate linear regressions for regions, with adjacent dis-

Fig. 9. Spatial differences in growth rates of larval cisco (*Coregonus artedii*), where growth rates were calculated by (a) length-to-age linear regressions (slope + standard error, SE) and by (b) back-calculating growth for the last 5 days before capture (mean + SE). Cisco were collected in 2000 from different distances from shore at Ontonagon (solid bars) and Houghton (open bars) in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.



tances from shore pooled to achieve sufficient sample sizes (Fig. 9). Estimated slopes (growth rates) decreased with distance from shore at Houghton, but not at Ontonagon (Fig. 9). Furthermore, when estimating models separately by region, an effect for distance from shore occurred at Houghton (multiple regression: $n = 84$, $r^2 = 0.67$, $b = -0.036$, and $P = 0.006$ for distance from shore \times age interaction), but not at Ontonagon (multiple regression: $n = 84$, $r^2 = 0.79$, $b = 0.00024$, and $P = 0.93$ for distance from shore \times age interaction).

Spatial differences in growth can similarly be assessed using estimated growth rates for the last 5 days before capture. This measure of growth more likely represents the habitat a larva was captured from, considering that cisco have the potential to travel great distances during their early lives. A similar multiple regression model ($n = 88$, $r^2 = 0.18$), including age as a covariate, showed an effect for distance from shore ($P = 0.04$) and not for region ($P = 0.11$); however, region interacted with distance from shore ($P = 0.04$),

as would be expected based on the previous growth results. A similar trend was observed graphically with plotted mean growth rates (Fig. 9), in which rates of recent growth decreased with distance from shore at Houghton, but not at Ontonagon. Separate analyses by region confirmed that the recent growth rate was statistically affected by distance from shore at Houghton (multiple regression: $n = 37$, $r^2 = 0.24$, $b = -0.024$, and $P = 0.03$ for distance from shore), but not at Ontonagon (multiple regression: $n = 51$, $r^2 = 0.13$, $b = -0.00002$, and $P = 0.99$ for distance from shore).

Relationship between growth rates and water temperatures

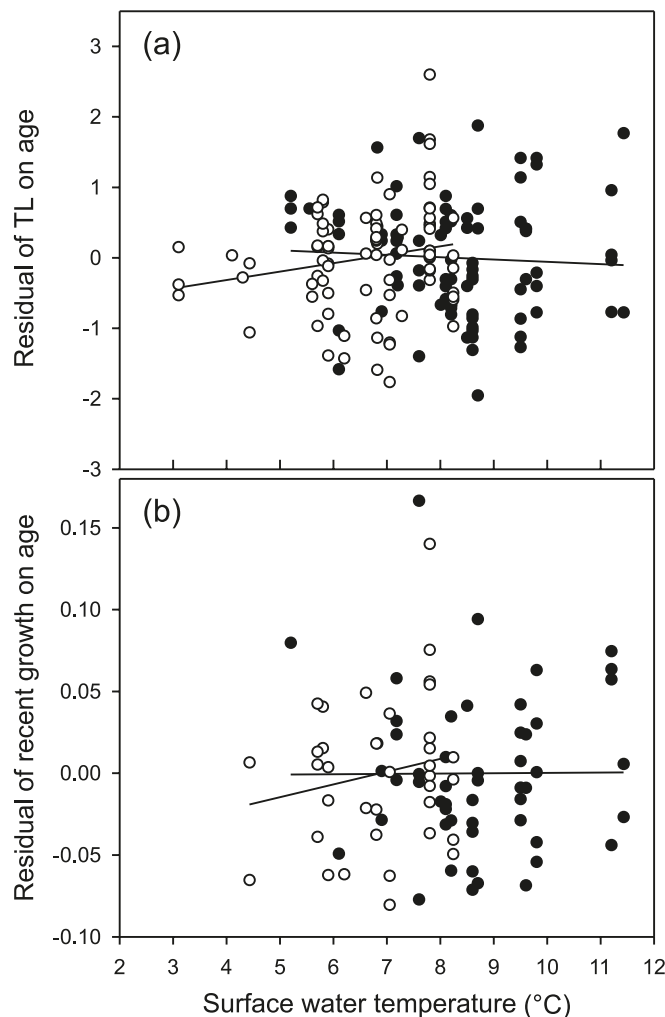
The spatial trend in growth rates at Houghton intuitively followed patterns of water temperatures, but further investigation was required to explain why such a trend was not seen at Ontonagon, where water temperatures also decreased with distance from shore. By regressing the length-to-age relationship on surface water temperature instead of distance from shore, it was observed that the growth rate decreased with decreasing temperatures more strongly at Houghton (multiple regression: $n = 84$, $r^2 = 0.65$, $b = 0.025$, and $P = 0.09$ for temperature \times age interaction) than at Ontonagon (multiple regression: $n = 84$, $r^2 = 0.81$, $b = 0.017$, and $P = 0.01$ for temperature \times age interaction), although strangely, the effect was more significant at Ontonagon. The same trend was observed for recent growth rates, but with less statistical significance, in which Houghton (multiple regression: $n = 37$, $r^2 = 0.15$, $b = 0.008$, and $P = 0.28$ for temperature) showed a stronger effect over Ontonagon (multiple regression: $n = 51$, $r^2 = 0.13$, $b = 0.00036$, and $P = 0.96$ for temperature). These trends can be visualized by plotting the residuals of length vs. age and recent growth rate vs. age against water temperatures, so that the data are standardized for differences in age (Fig. 10). From this figure it can be seen that (i) Houghton and Ontonagon contained different ranges of temperatures and (ii) growth rate tended to decrease with temperature at the colder temperatures observed at Houghton and was unaffected by temperature at the generally warmer temperatures observed at Ontonagon.

Finally, the data set was divided, not by region as done previously, but by proposed threshold temperatures, below which temperature was expected to inhibit growth relative to growth above the proposed threshold. The greatest effect of temperature was below a proposed threshold of 8.5°C with the length-to-age approach to estimating growth rate (multiple regression: $n = 128$, $r^2 = 0.65$, $b = 0.027$, and $P = 0.02$ for age \times temperature interaction) and below 8°C with the back-calculated approach (multiple regression: $n = 45$, $r^2 = 0.08$, $b = 0.013$, and $P = 0.11$ for temperature) (Fig. 11). But overall there was still great variation in growth rates at given temperatures, even after the data were standardized for differences in age.

Discussion

The distribution patterns of cisco followed what would be expected if larvae were being transported by currents from productive spawning regions in western Lake Superior (Goodyear et al. 1982). It is also possible that some larvae originated from historic spawning grounds from within the

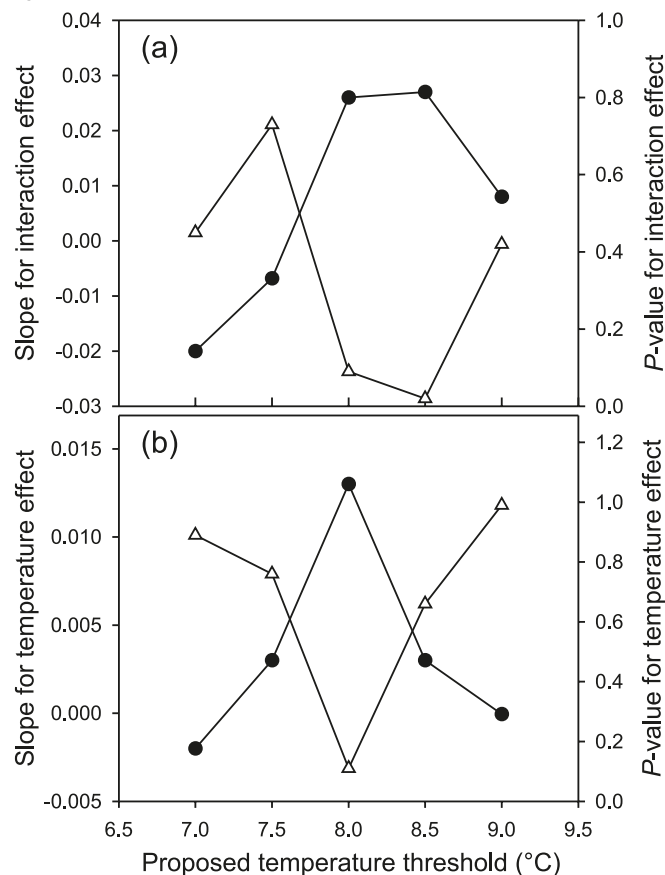
Fig. 10. Relationship between growth rate of larval cisco (*Coregonus artedii*) and surface water temperature. Cisco were collected in 2000 from different distances from shore at the Ontonagon (●) and Houghton (○) transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Growth rates were estimated by (a) length-to-age (TL, total length) linear regressions and by (b) back-calculating growth for the last 5 days before capture for each region. The effect of age was standardized by presenting the residuals of each model. Residuals were calculated separately for each region.



study area, at either Ontonagon or Houghton. It was expected that larvae would be more abundant nearer to spawning grounds and less abundant as they disperse away from them. In fact, the greatest densities were observed far offshore at Ontonagon, and Ontonagon generally had higher densities than Houghton. The high-density patch encountered at 7–13 km from shore at Ontonagon consisted of larvae that were younger than those captured nearer to shore. However, these offshore larvae did not hatch recently, but instead averaged slightly less than 30 days of age. Therefore, even if the offshore larvae were encountered at a high concentration akin to a hatching location, these larvae also had sufficient time to travel from some distant location.

The progression of hatch dates with subsequent cruises also supports the conclusion that cisco were transported

Fig. 11. Regression coefficients (slopes, ●) and *P* values (Δ) for linear regression models below proposed threshold temperatures. For (a) regression-estimated growth, slopes and *P* values are for the age × temperature interaction; for (b) back-calculated recent growth, slopes and *P* values are for the temperature main effect. Age was also included in the back-calculated model as a covariate.



eastward, following the general flow of currents. The lack of early-hatch larvae in samples from later cruises can be explained by larvae being transported from the study area or by the following alternative mechanisms. First, because early-hatch larvae would have to survive for a longer duration to still exist during later dates compared with recently hatched larvae, a greater cumulative mortality for early-hatch larvae could account for their absence at later dates (Campana and Jones 1992). Second, early-hatch larvae may have grown beyond the size range for which they are susceptible to capture with ichthyoplankton nets (Karjalainen and Viljanen 1992). In contrast, the lack of late-hatch larvae in samples from earlier cruises can not be explained by these alternative mechanisms. The late-hatch larvae would have been more susceptible to capture by plankton nets and would have undergone less cumulative mortality on earlier dates than on later dates. Therefore, the presence of late-hatch larvae only on the later sampling dates, in conjunction with an increase in mean hatch date with subsequent cruises, further supports the conclusion that larvae were transported from adjacent regions. In addition, a cruise covering Ontonagon and Houghton on 27–29 April captured only two larvae with 2715 m³ of water sampled even though this cruise occurred during the peak of the hatch.

The spatial patterns of larvae of different hatch periods point to offshore Ontonagon as the location where late-hatch larvae first arrived in the study region. From there, they appeared to have dispersed inshore and up the Keweenaw coast to Houghton. In addition, early-hatch larvae were concentrated inshore during earlier cruises and were rare or absent on later cruises. Therefore, it appeared that cisco moved progressively through the study region, and by the time the late-hatch larvae arrived in inshore areas, early-hatch larvae were almost absent.

Wind-driven currents have been found to be important for transporting fish larvae in many large aquatic systems (Werner 2002). For example, Fechtelm and Griffiths (1990) studied the 600–700 km westward transport of Arctic cisco (*Coregonus autumnalis*) larvae along the Alaskan and Canadian Beaufort Sea coast. They found that years of moderate to high recruitment were associated with strong easterly winds during summer, and years of poor recruitment occurred when easterly winds were weak. Anomalous winds can also disrupt a transport system, as was documented by Bailey et al. (1999) for walleye pollock (*Theragra chalcogramma*) larvae in Shelikof Strait, Gulf of Alaska, during 10 days in May 1996. Recently, the offshore transport of yellow perch (*Perca flavescens*) larvae in Lake Michigan has been documented by Dettmers et al. (2005) and modeled by Beletsky et al. (2007). Fishes may even be adapted to spawn at particular locations and times so to better ensure that their eggs or larvae will be successfully transported to nursery grounds (Parrish et al. 1981).

Once in the study region, cisco tended to congregate at Ontonagon and at inshore areas at both Ontonagon and Houghton. The larvae persisted at Ontonagon later in the season than at Houghton, but if they were only drifting passively through the study region, Houghton should have contained the last of the larvae. Likewise, inshore areas contained a concentration of older larvae that unlikely would have formed and persisted if larvae were only passive drifters. They seemed to be able to remain in the study region for a longer duration when at inshore locations or at Ontonagon, where they likely avoided most of the influence of the Keweenaw Current, compared with larvae at farther distances from shore or farther along the Keweenaw coast where waters deepen and the current intensifies (Niebauer et al. 1977; Green and Terrell 1978). In fact, larvae at Houghton on 5–7 June were rarely encountered, despite extensive sampling from both north and south transects from distances of 0.5–7.0 km from shore, and during the last cruise, Houghton samples were completely devoid of cisco. Therefore, after a period of dispersal, cisco appeared to have settled into nearshore areas where they probably had more control of which habitat to occupy, and more larvae remained near Ontonagon.

Otolith analysis provided estimates of hatch dates and growth rates directly from age, which was not previously feasible for cisco without a validation study (Oyadomari and Auer 2007). The estimated hatch dates, primarily from mid-April to early May, corresponded to what was observed previously with distribution data from western Lake Superior (Hatch and Underhill 1988) and from the St. Mary's River (Jude et al. 1998). Estimated mean growth rates of 0.12–0.22 mm·day⁻¹ were comparable with a mean estimate

of 0.27 mm·day⁻¹ for the St. Mary's River (Jude et al. 1998), but were lower than an estimate of 0.69 mm·day⁻¹ for western Lake Superior by Hatch and Underhill (1988), although they believed this was an overestimation.

Larval growth rates were compared in order to determine if larvae received some benefit from remaining at inshore locations. It was expected that growth would be higher in the warmer inshore waters, especially at Ontonagon. Morphological characteristics alone indicated that inshore-captured larvae were larger than larvae caught at farther distances from shore, and sampling in this study region during previous years revealed a similar trend (Oyadomari and Auer 2004). But then age explained much of this difference, with inshore larvae being correspondingly older. When analyzing for differences in growth rates, while accounting for the variation in age, only the Houghton catches displayed an offshore trend, in which growth was slower at farther distances from shore. The growth rates of the offshore larvae at Houghton appeared to have been suppressed from what was achieved at Ontonagon.

The difference between regions in the offshore relationship of growth rate could be explained by temperature differences, whereby water temperatures at Ontonagon were usually high enough not to limit growth. In the laboratory, McCormick et al. (1971) observed that cisco growth increased with temperature in the range 3–18 °C; however, mortality started to increase substantially from approximately 13 °C. The final preferendum for cisco is 9–14 °C (Wisner and Christie 1987); thus, it was reasonable to find that temperature inhibited growth below 8 °C. Temperature may also explain the increase in growth rate with later hatch dates. Because of seasonal warming, larvae that hatched later would have spent less time swimming in colder waters. However, there was still great variation in the distributional patterns. Such variation probably resulted from the fact that larvae were moving and that the temperatures at which they were captured may not have represented the predominant temperatures they experienced throughout their young lives.

Water temperature has been shown to be important for growth in other *Coregonus* species as well. Early growth of the common whitefish (*Coregonus lavaretus*) from Lake Constance (Germany) closely tracked spring warming and not zooplankton abundance (Eckmann and Pusch 1989; Rey and Eckmann 1989), and subsequent year-class strength was associated with early thermal stratification (Eckmann et al. 1988). Earlier-hatched bloater (*Coregonus hoyi*) larvae from Lake Michigan grew slower, and consequently suffered greater mortality, probably owing to increased predation (Rice et al. 1987).

At higher temperatures, another factor, most likely food resources, may have limited growth via an increased metabolic demand. Larvae at higher temperatures would have to consume more food to achieve the same growth rate at a lower temperature (Houde 1989). Therefore, at higher temperatures a higher growth rate can only be obtained with an adequate food supply. Increasing metabolic requirements with seasonal warming may explain why larvae probably depart inshore areas by late June to early July (Clady 1976; Hatch and Underhill 1988; Oyadomari and Auer 2004).

With faster growth within a suitable habitat, cisco larvae would have a greater probability of survival. In general, lar-

vae that obtain larger sizes have greater swimming abilities, are more successful at feeding, are more resistant to starvation, and are less susceptible to predators (Miller et al. 1988; Jones 2002). Larger-sized cisco in particular have been shown to better survive a simulated winter (Pangle et al. 2004). Because of the lack of a sufficient number of older larvae, size-selective mortality could not be evaluated with otolith analysis for cisco, but mortality in many species has commonly been shown, with otolith analysis, to be size dependent, whereby smaller larvae or juveniles suffer greater mortality (e.g., Post and Prankevicius 1987; Meekan et al. 1998; Gronkjaer et al. 2004).

A strong year class requires successful reproduction, followed by high survival of eggs, larvae, and juveniles (Houde 1987). It is only after hatching that offspring have some control over their survival. Larvae can increase their probability of survival by inhabiting areas that foster faster growth and contain fewer predators (Simpson 1987). Reaching such areas, however, may be impossible for larvae with limited swimming abilities if it were not for the aid of longshore currents. The wind-driven currents in Lake Superior have potential to disperse larvae away from spawning concentrations and into adjacent areas. If larvae are not dispersed, they may suffer greater mortality by attracting predators or by competing for limited food resources. Because of its large size, Lake Superior appears to behave more like an ocean than a lake. Accordingly, the role of meteorological and hydrodynamic processes controlling transport should be explored by recruitment studies of fishes with pelagic larvae, such as cisco.

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